THE DISAPPEARANCE OF LITTER IN MULL AND MOR IN CONNECTION WITH WEATHERCONDITIONS AND THE ACTIVITY OF THE MACROFAUNA

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Introduction

One of the characteristic distinguishing features of mull and mor in forests is the absence of litter at the beginning of leaf fall in the first type and the presence of a litter layer of varying thickness at the same time in the latter. This does not necessarily mean that the yearly disappearance of litter in the mull is greater than in the mor. In a previous publication (WITKAMP and VAN DER DRIFT, 1961) it was mentioned that 80% of the litter fallen on a cleared surface in a calcareous mull had disappeared already in April, whereas in a nearby mor only 30% of about the same amount of litter had disappeared at that time. It seems evident that the pattern of litter attack is quite different in mull and mor. But also from one year to the other there are great differences within each of the types.

To elucidate these differences litter disappearance was measured from 1957 upto 1962 in a calcareous mull and in a mor both in a mixed hardwood coppice on moist sandy soil. A concise description of the experimental field, Hackfort, at about 6 km SE from Zutphen is given by WITKAMP (1960) and MINDERMAN (1960). In this paper the rate of disappearance will be compared with the main meteorological factors temperature and precipitation.

The different rates of litter breakdown in mull and mor may be related to differences in fauna composition but also to differences in activity pattern of saprophagous species.

During winter, spring and summer of the year 1962 the relative abundance of saprophagous macrofauna and the periodicity of its activity was studied in each of the types.

Litter disappearance and weather conditions

From 1957 on to 1962 in each of the types at least 10 samples of $\frac{1}{4}$ m^2 were taken on characteristic spots to evaluate the amount of litter. Sampling was performed at dry weather in September, just before leaf fall and in December, when leaf fall was completed. The samples were selected carefully for the leaf litter only; twigs, fruits, bark and occasionnally roots were rejected. Samples were weighed in the field and returned with exception of a small subsample for determination of the water-content (air dry). In September only the old leaf litter was selected. The few, newly fallen leaves were rejected. In December both the old leaf litter and the newly fallen leaves were weighed separately. In the first two years the leaf fall was determined in bags of cloth with openings of $\frac{1}{2}$ m^2 in which the leaves were collected once a week.

The results are given in the upper part of Fig. 1. The data from mull are given in solid lines, those from mor in broken lines. The amount of old litter is given in the hatched parts of the columns, the amount of freshly fallen litter in the white parts. The slope of the connecting lines indicate the rate of disappearance from December up to September. The figures on these lines give the absolute amount of litter disappeared.

To compare the rate of litter disappearance with the general weather conditions the monthly averages of day-time airtemperature (means of 8.00, 14.00 and 19.00 readings) and the monthly precipitation both from the nearest climatological station of the Royal Netherlands Meteorological Institute are presented in the lower part of Fig. 1. The data of this station (Almen at about 6 km in N.E. direction from the experimental field) are graphed with the 10 years average (1951—1960) to show the relative tempeture and moisture conditions of the successive years. Positive deviations from the average, hot and wet periods, are hatched vertically. Negative deviations, cold and dry periods are hatched horizontally.

Disappearance in mull

In mull the litter disappearance from December onto September ranged from 320—400 g per m^2 in five out of the six years. In 1959 only 230 g disappeared, which may certainly be connected with the high temperature and the extreme drought. There was a certain litter accumulation compared with the preceeding year and this accumulation could not be compensated

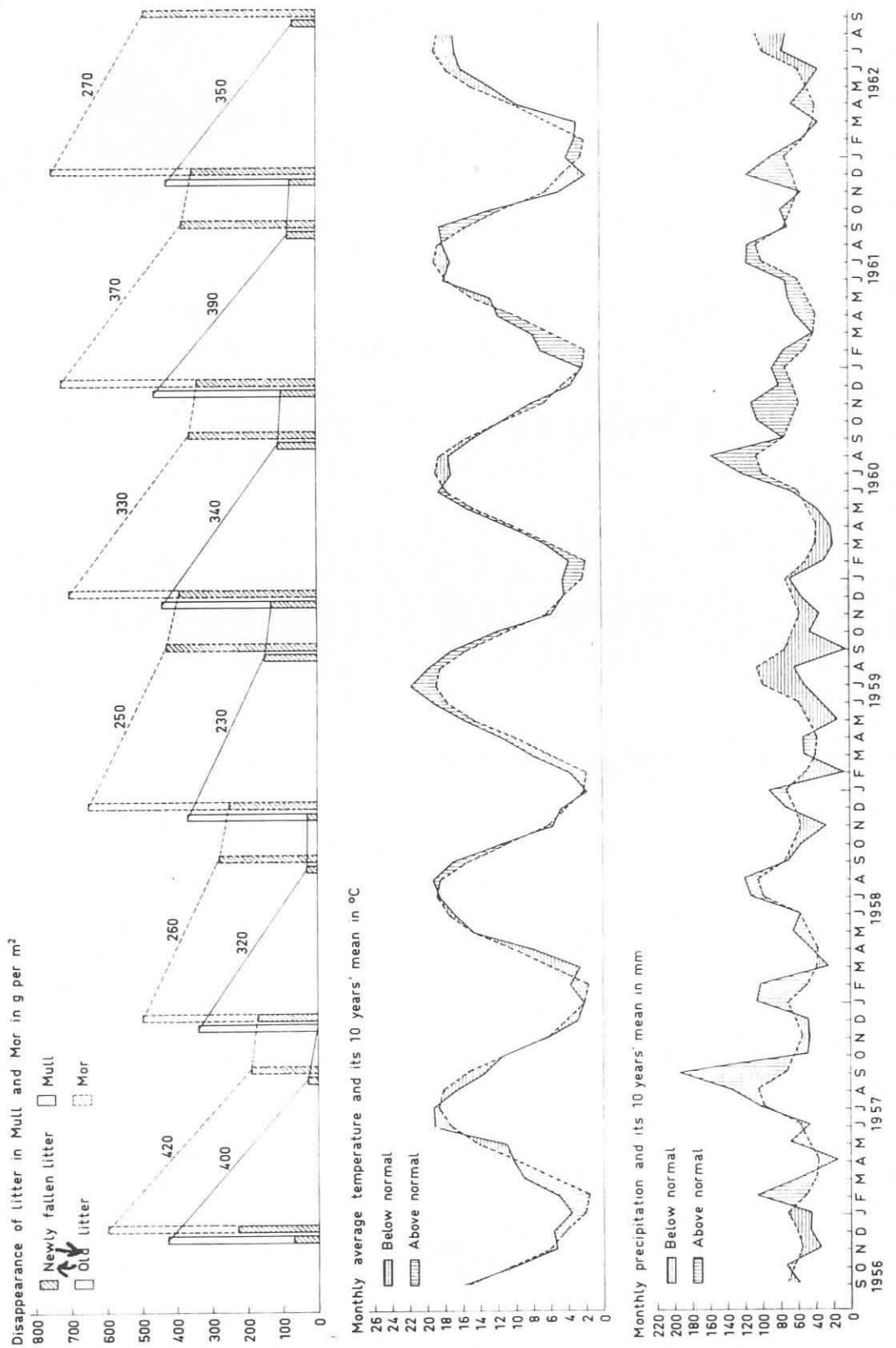

Fig. 1. Disappearance of litter and monthly averages of temperature and precipitation.

completely by greater attack in the next three years. It seems that the varying weather conditions in 1957, '58, '60, '61 and '62 did not substantially influence the disappearance in the mull. However it must be noted that in 1957 and in 1958, when detailed observations on litter disappearance during the year were made, there was a clear difference in time with respect to reaching the minimal amount of litter. This minimal amount — about 30 g per m^2 — means that the litter layer is disrupted and the remaining fragments are subject to strong desiccation, which inhibits further attack. In 1957 this minimal amount was reached, after a disappearance of 400 g, already in June. In 1958 with less favourable weather conditions — lower temperature, less precipitation — the same amount was not reached before September and only 320 g had disappeared. It seems that in 1957 the amount of litter was the limiting factor in the litter decaying process, in 1958 it were the weather conditions. In 1960, '61 and '62 the amount of remnants was greater than in 1957 and 1958. Apart from weather conditions, the much lower densities of saprophagous fauna (table 1), consequence of the dry summer of 1959, must be taken into account.

TABLE 1. Approximate densities per m^2 of some saprophagous groups before and after the dry summer of 1959

	Mull		Mor	
	1957	1961	1957	1961
Lumbricidae	100	50	60	40
Pulmonata	20	30	5	—
Isopoda	40	10	20	5
Diplopoda	100	40	35	10
Tipulidae	80	30	5	5
Enoicyla	900	—	—	—

Disappearance in mor

In the mor the litter decay is never limited by the amount of litter, moreover the fauna is less influenced by the dry summer of 1959 (table 1). So a better correspondence between litter disappearance and weather conditions may be expected. Indeed small amounts disappeared in 1958 and 1962 with cold summers and rather small precipitations. Still smaller was the disappearance in the dry and hot year 1959. The greatest amounts dis-

appeared in 1957 and 1961 with rather similar weather conditions: warm spring, cool summer and rather great precipitation. The intermediate position of the litter disappearance in 1960 is somewhat puzzling: the dry and warm weather in the first half of the year would have made one to expect a smaller disappearance of litter.

If we will compare the litter balance in mull and in mor we must first pay attention to the litter production in both types. In the mull the average amounts 332 g per m^2, ranging between the rather narrow limits of 305 and 350. In the mor the average production of litter is 354 g per m^2 with much wider extremes: 310 and 400. Apparently the litter production in the mor is less stable than in mull. In only one year (1957) the production was less than in mull. In both types the litter production was smallest in the dry year 1959. In the mor it was 12% less than the six years average, in the mull 8%.

Contrary to the litter production the average litter disappearance was greater in the mull (338 g per m^2) than in the mor (317 g per m^2). The 1959 figures excluded, the range in the mull (320—400) was again much smaller than in the mor (260—420). In two years, 1957 and 1959 the litter disappearance was greater in the mor than in the mull. In the favourable year 1957 this may be attributed to the limiting influence of the amount of litter in the mull, in the unfavourable year 1959 to the fact that the thick litter layer in the mor is less susceptible for desiccation than the thin layer in the mull. Litter disappearance was smallest again in the dry year 1959. The inhibiting influence of the weather conditions in this year were greatest in the mull. Litter disappearance was here 32% less than the average, in the mor it was 21% less.

Due to the differences in average litter production (in mull 6% less than in mor) and in average litter disappearance (in mull 7% greater than in mor), there is a big difference in the overall litter accumulation over the six years in the two types. In the mull there is no accumulation at all (compare the mull columns in September 1962 with that in December 1956), indeed there may be some overall decrease as the average litter disappearance is somewhat greater than the average litter production. In the mor, however, there is a distinct accumulation. From December 1956 onto September 1962 there was an increase of about 250 g per m^2. The difference in overall accumulation in the two types is about equally caused by the greater litter production, and the smaller litter disappearance in the mor.

From the diagram and from what is said above it is clear that the

absence of overall litter accumulation in the mull does not mean that there was no incidental accumulation. In fact there was accumulation in 1959 but this was largely compensated in the next years. So in mor there were years without accumulation (1957, 1960), but the great accumulation in 1959 for which was not compensated sufficiently in the next years resulted in the great overall accumulation.

The differential influence of weather conditions via biological activity on litter disappearance in mull and mor may be of importance in the maintenance of these soil types and even in their development.

Saprophagous macrofauna and its activity pattern

The disappearance of litter in forests is mainly caused by the feeding activity of macrofauna species: earthworms, slugs, snails, Isopods, Millipedes, Insect larvae. Though the activity of smaller animals, Enchytraeids, Oribatei, Collembola and the activity of microorganisms, Protozoa, Fungi, Bacteria certainly aids in the attack of the litter, it does not as such substantially contribute to the removal of the leaf litter from the floor.

In 1962 the relative abundance and the seasonal activity of the macrofauna in mull and mor was studied. It was hoped for favorable weather conditions giving rise to a rapid litter disappearance in mull as occurred in 1957. In that case a decreasing animal activity might be expected in mull against a rather constant activity in mor. Unfortunately the weather turned out to be exceptionally cold and rather dry (see Fig. 1) and so the litter layer in the mull disappeared only slowly. That is the reason why the investigations yielded only some feeble suggestions for differences in activity pattern in mull and mor.

As the best approximation both for the relative abundance and the seasonal activity, the number of animals observed by four trained people, searching the litter layer during half an hour was chosen. In this time a track of about 1 m wide and 6—10 m long was inspected. It is assumed that all animals observed at this superficial inspection were actually feeding in the litter layer or did feed there shortly before. Observations were made at about fortnightly intervals during the morning with dry and not too cold weather. Personal differences between collectors were only of minor importance. The results are presented in Fig. 2. In addition to the results from the sites mentioned in the previous section (calcareous mull and mor), those from a third site (comprising Minderman's subtypes acid mull and

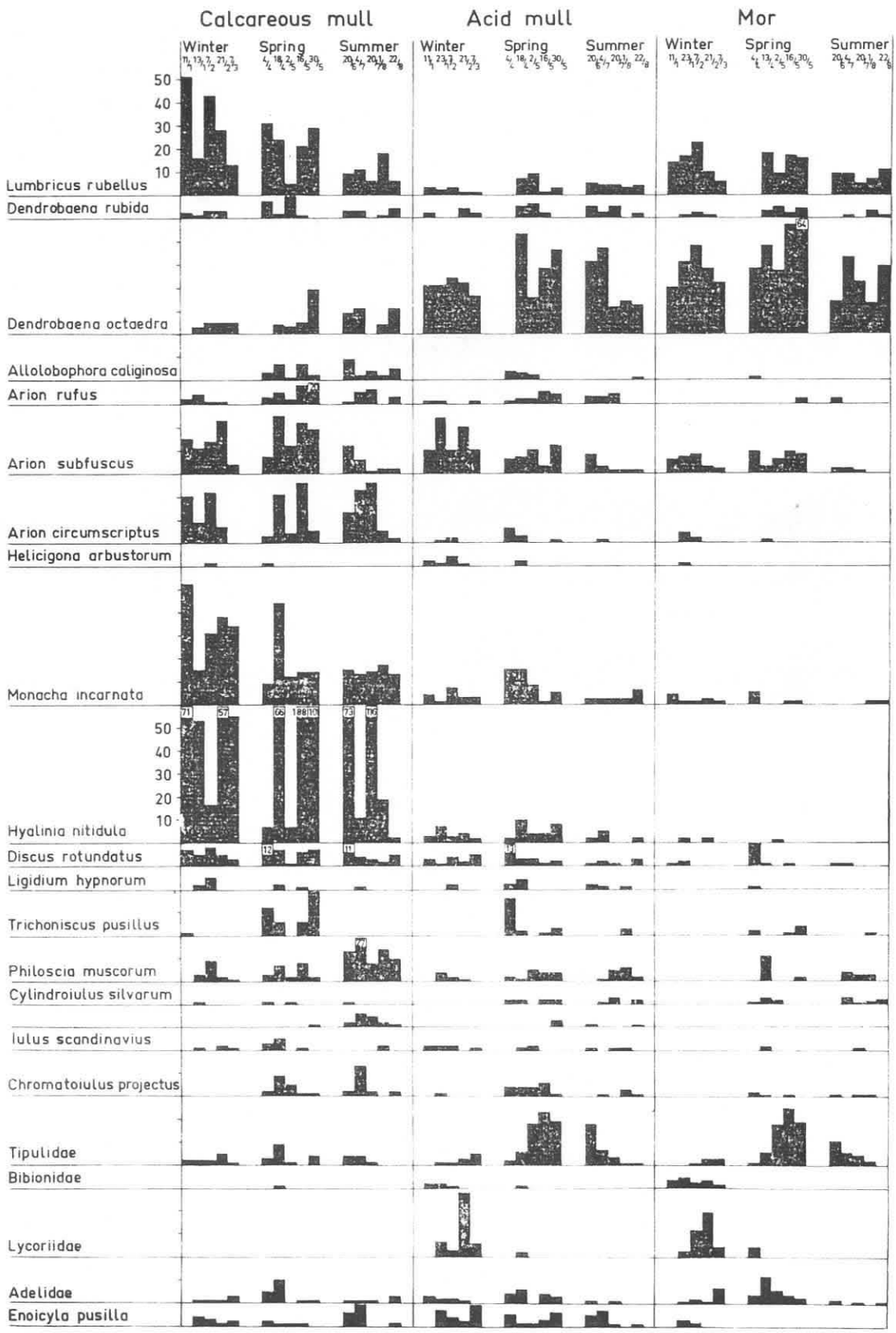

Fig. 2. Saprophagous macrofauna collected in two man-hours.

mull rich in litter and designated here as acid mull) in the same forest are included. Both with respect to litter disappearance as to fauna composition this site is a transitional one. Local differences within each type may have caused such discordances as shown in *Hyalinia nitidula*.

The differences in macrofauna composition are obvious. Many species occurring abundantly in the calcarous mull are less abundant in the acid mull and are scarce in the mor: *Allolobophora caliginosa*, *Arion rufus*, *A. subfuscus*, *A. circumscriptus*, *Monacha incarnata*, *Hyalinia nitidula*, *Discus rotundatus*, *Trichoniscus pusillus*, *Philoscia muscorum*, *Ligidium hypnorum* *Chromatoiulus projectus*, *Cylindroiulus nitidus*, *Julus scandinavius*, and *Enoicyla pusilla*. This difference seems to be an important cause for the decreasing rate of litter disappearance in these sites. The reverse is only the case with some species: *Dendrobaena octaedra*, Tipulid larvae, Bibionid larvae and Lycoriid larvae, whereas only *Dendrobaena rubida* and Adelidae larvae are about equally distributed over the three sites.

Species, which suggest a decreasing activity in the calcarous mull site are *Lumbricus rubellus*, *Arion subfuscus* and *Monacha incarnata*. Constant activity at a rather high level in mor is shown by *Lumbricus rubellus* and *Dendrobaena octaedra*. Only in the case of *Lumbricus rubellus* there was some indication of difference in activity pattern in the calcareous mull site at the one hand and the other two sites at the other.

Conclusion

Meteorological conditions apparently influence litter breakdown. Precipitation, so moisture conditions, seems to be of more importance than temperature, though soft winters and warm springs, when moisture does not act as limiting factor, may accelerate breakdown.

The actual agents in this relationship are the soil organisms of which the macrofauna is mainly responsible for the removal of the litter. Its urgent moist requirements and its activity in temperate winters are in accordance with the mentioned meteorological influences on litter breakdown.

Actual litter disappearance in mor can exceed the disappearance in mull if in the latter the litter layer is removed before the next leaf fall and favourable conditions for attack sustain. Under unfavourable conditions when litter disappears slowly, in mull disappearance can be completed before next leaf fall, whereas in mor accumulation occurs. If in mull accu-

mulation occurs this is to a much lower extent and it can be compensated in the next years much easier than in mor.

Apart from the qualitatively and quantitatively richer saprophagous macrofauna in mull the seasonal activity pattern may be distinct from that in mor. The analysis of this pattern however is hampered by the unpredictability of the weather.

Summary

Litter production and litter disappearance was investigated during a 6 year period in two sites of a mixed hardwood coppice on sandy soil, with mull and mor floortypes. Correlations with general weather conditions are described. Relative abundance and seasonal activity of the saprophagous macrofauna in mull and mor in the last year were studied.

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